

The Homogocene: a research prospectus for the study of biotic homogenisation

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Abstract

In an era of global change, the process of biotic homogenisation by which regional biotas become more similar through time has attracted considerable attention from ecologists. Here, a retrospective look at the literature is taken and the question asked how comprehensive is the understanding of this global phenomenon? The goal is to identify potential areas for additional and future enquiries to advance this research frontier and best ensure the long-term preservation of biological diversity across the world. Six propositions are presented here to; (1) broaden our geographic and taxonomic understanding, (2) diversify the spatial and temporal scales of inquiry, (3) reconcile past and embrace new approaches to quantification, (4) improve our knowledge of the underlying drivers, (5) reveal the conservation implications and (6) forecast future homogenisation. It is argued that significant progress in the understanding of the causes, consequences and conservation implication of biotic homogenisation will come by integrating concepts and approaches from ecology, evolution and conservation across a hierarchy of spatial and temporal scales.

Keywords

beta-diversity, biodiversity conservation, species introductions, urbanisation, taxonomic, functional, phylogenetic similarity

Introduction

Since its first formal definition close to two decades ago, biotic homogenisation – referring to the increase in floral and faunal similarity amongst communities or decrease in beta-diversity over time (McKinney and Lockwood 1999) – has been the focus of considerable

attention by ecologists (Fig. 1). This prominence in literature is not entirely surprising; many of the conservation challenges facing society necessitates broadening our science from understanding individual species loss to anticipating multi-faceted changes to biodiversity (Naeem 2013, Dornelas et al. 2014, McGill et al. 2015, Socolar et al. 2016). The notion that the loss of native species concurrent with the introduction and establishment of non-native species aided by humans will continue relatively unabated into the future, has prompted many to herald the coming era in Earth's history as the 'Homogocene'. The world envisioned is one where considerable reshuffling of biotas will result in significant ecological and evolutionary consequences (Olden et al. 2004) and may ultimately flavour the manner in which humans experience the natural world (Olden et al. 2005).

Although there is little debate that species extinctions and invasions have fundamentally altered patterns of biogeography (Dirzo et al. 2014, Ceballos et al. 2015), a literature review demonstrates that the number of articles referring to biotic homogenisation is seven times greater than the number of articles providing quantitative estimates of changes in community similarity (Fig. 1). This inevitably leads to the question: how comprehensive is our understanding of biotic homogenisation? What is known is that across all empirical studies, biotic homogenisation was reported more often (odds ratio = 1.6) than biotic differentiation or no change in community similarity through time (Fig. 2). A closer look at the data reveals that the overall homogenisation effects were driven largely by studies in the Nearctic region, whereas the results are somewhat more variable and sparse for other biogeographical zones. Similarly, estimates of biotic homogenisation vary considerably within and amongst taxonomic groups (Fig. 2), which reflects, to some extent, the rich variety of definitions and methods used (discussed below).

Despite the apparent pervasive, but notably uncertain, evidence for biotic homogenisation across the Earth, many questions remain unanswered. Are changes in community similarity permanent or transient? What can past trends in biotic homogenisation tell us about the likely future of biodiversity? How can this body of knowledge help to shape conservation policy and management decisions? While recent years have seen progress in addressing these and other more advanced questions, it is argued that additional and more targeted scientific inquiry is needed to advance the understanding of biotic homogenisation and best ensure that conservation efforts succeed in preserving the antiquity of biological life across the world. By taking a retrospective look at the last 20 years of scientific inquiry, a series of propositions is presented that seek to stimulate further discussion and advance this research frontier.

Broaden our geographic and taxonomic understanding

A careful reflection of the published literature reveals that significant geographic and taxonomic biases currently flavour our perception of the magnitude and extent of biotic homogenisation. Perhaps not surprisingly, biotic homogenisation has been studied to a much greater extent in the Northern hemisphere, with close to three-quarters of the research conducted in the Palearctic (42 %) and Nearctic (30 %) regions (Fig. 1). This pattern

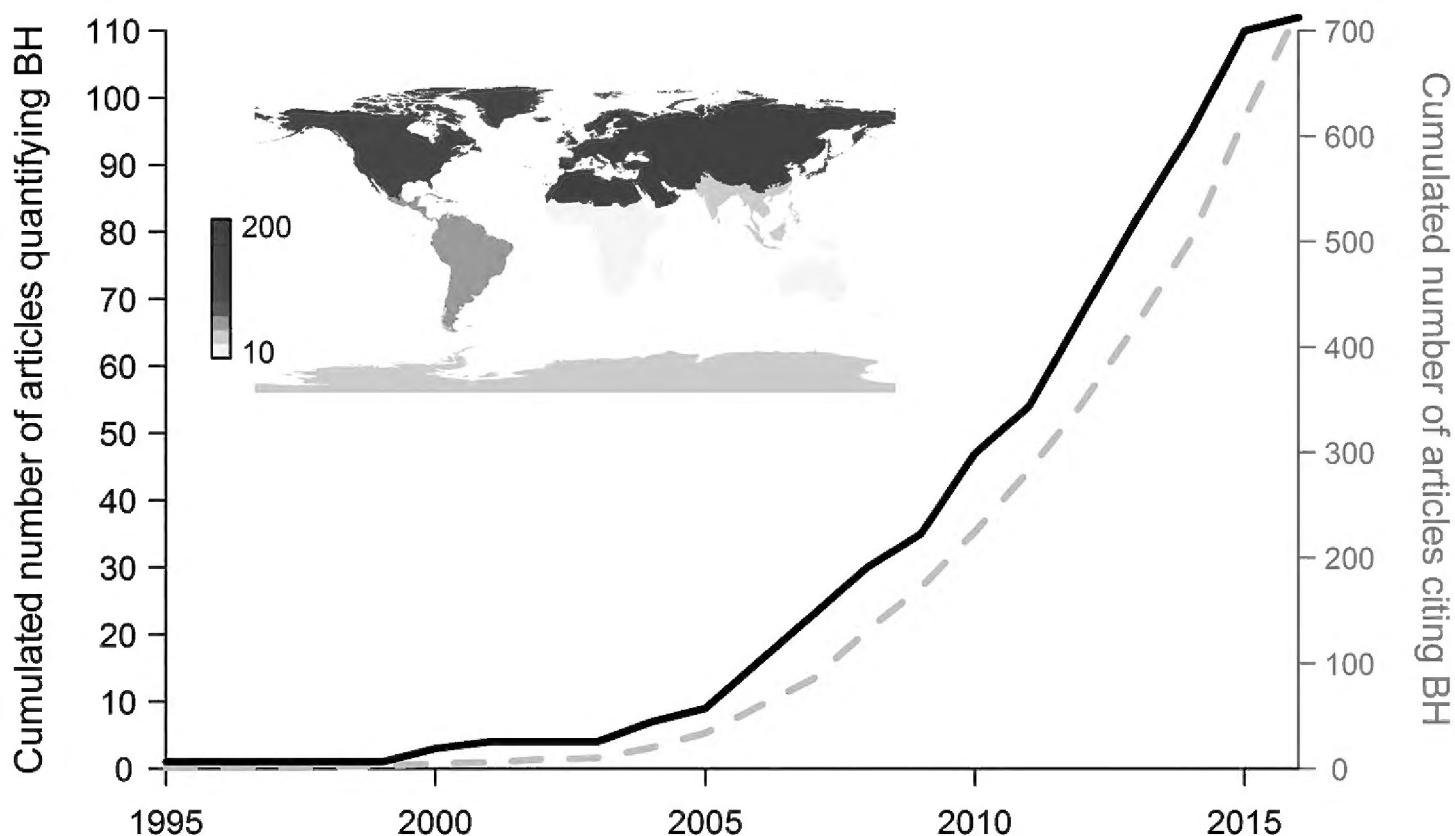


Figure 1. Cumulative number of published articles that quantified biotic homogenisation (BH) (left axis; black line) based on a literature search using “(biotic OR taxonomic OR functional OR phylogenetic) AND (homogenization or homogenisation) AND (similarity OR Jaccard OR Sørensen OR Sørensen OR Bray-Curtis OR Raup-Crick)” as key terms in ISI Web of Knowledge and Google Scholar, compared to the cumulative number of articles containing the term “biotic homogenization” in the Abstract or keywords (right axis; grey dotted line) resulting from a broader search of the literature using “biotic homogenization” OR “biotic homogenisation”. Only those studies that quantified changes in beta-diversity over time (i.e. the definition of homogenisation) were included. The inset illustrates the number of reported estimates of biotic homogenisation across all studies according to the major biogeographical zones.

mirrors similar geographic biases in the study of invasive species (Pyšek et al. 2008) and biodiversity (Trimble and van Aarde 2012) and also undoubtedly reflects the effects of under-reporting of no change or differentiation. Terrestrial plants and freshwater fishes are the most frequently studied taxonomic group, whereas birds, mammals and other vertebrate and invertebrate groups were less often evaluated (Fig. 2). For example, only recently have studies examined taxa such as marine corals and freshwater molluscs and zooplankton.

Cross-taxonomic studies of biotic homogenisation also remain almost non-existent (representing a mere 4 studies); yet they remain critical for gaining a broader systems-level perspective. For example, Carvalheiro et al. (2013) showed concurrent patterns of homogenisation for plants and flower-visiting insects in north-western Europe over a 70-year period, suggesting the importance of biotic interactions in shaping changes in community similarity through time. Expanding geographic and taxonomic understanding of the homogenisation process are ripe areas of future investigation. It is believed that, by concentrating on unstudied regions and taxa, rather than bolstering past research foci, it will be possible to better generalise our knowledge regarding the causes and consequences of biotic homogenisation.

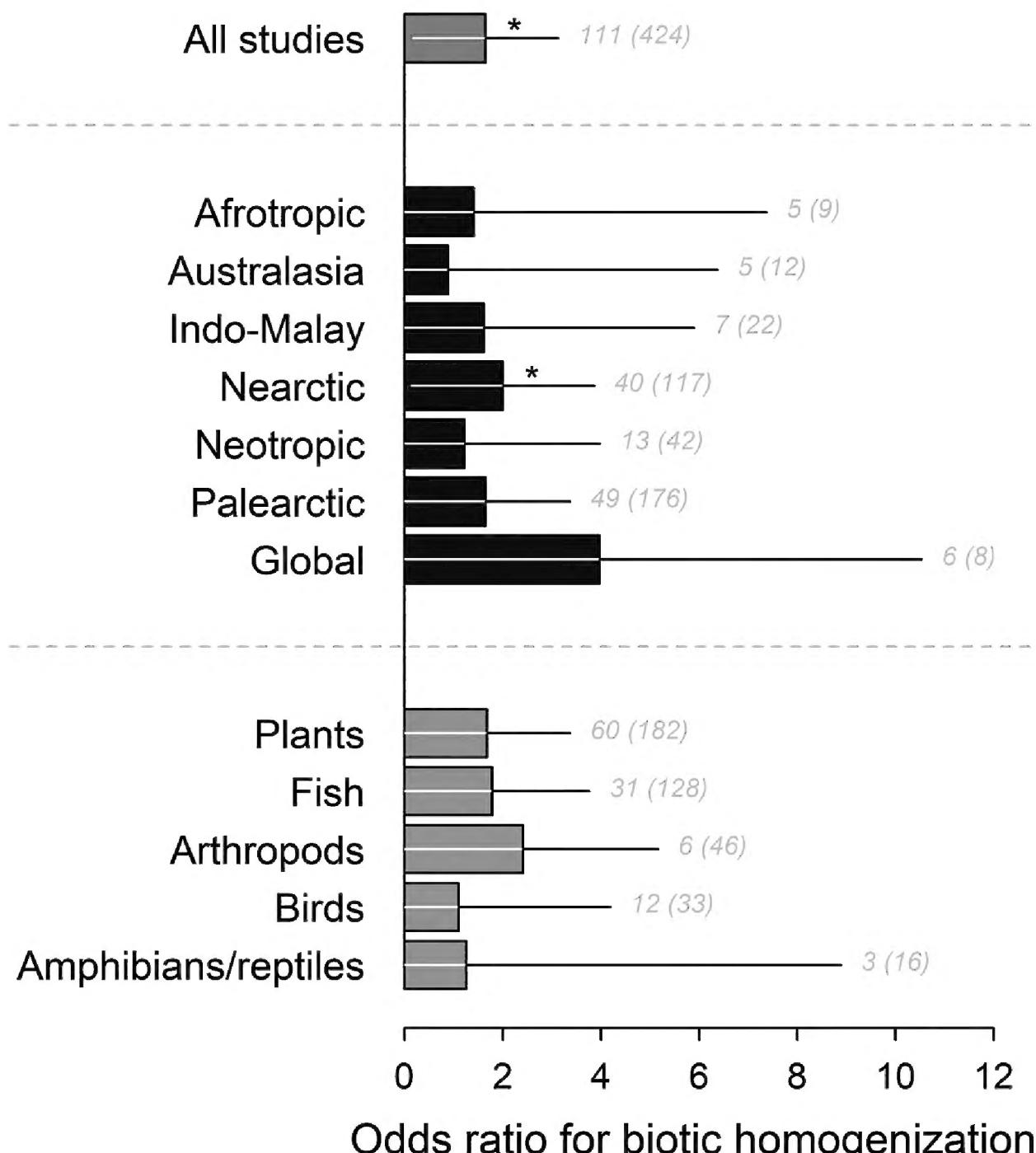


Figure 2. Estimated odds ratio and associated 95 % confidence intervals for the demonstration of biotic homogenisation across all studies assessed (top) and studies organised by biogeographic areas (middle) and taxonomic group (bottom). Asterisks indicate statistically significant effects ($p<0.05$). Odds ratios were estimated from generalised linear mixed effect models using a binomial error structure where studies were coded 1 if they reported biotic homogenisation or 0 if they reported no significant change or biotic differentiation. Additionally, potential variations due to methodological factors were accounted for by specifying *article identity*, *spatial grain*, *spatial extent*, *facet*, *temporal extent* and *metric* as random effects in the models. Numbers in grey indicate the number of published articles for each group included in the models. Groups in middle and bottom panels represented by less than two articles were excluded from the analyses.

Diversify the spatial and temporal scales of inquiry

It was found that spatial scales of investigation vary extensively, with studies quantifying biotic homogenisation at local ($<100 \text{ km}^2$) to continental or global extents according to various spatial grains ($100\text{--}1,000 \text{ km}^2$) (Fig. 3). Studies quantifying biotic homogenisation at large spatial extents are exclusive to plants, fishes and birds, whereas

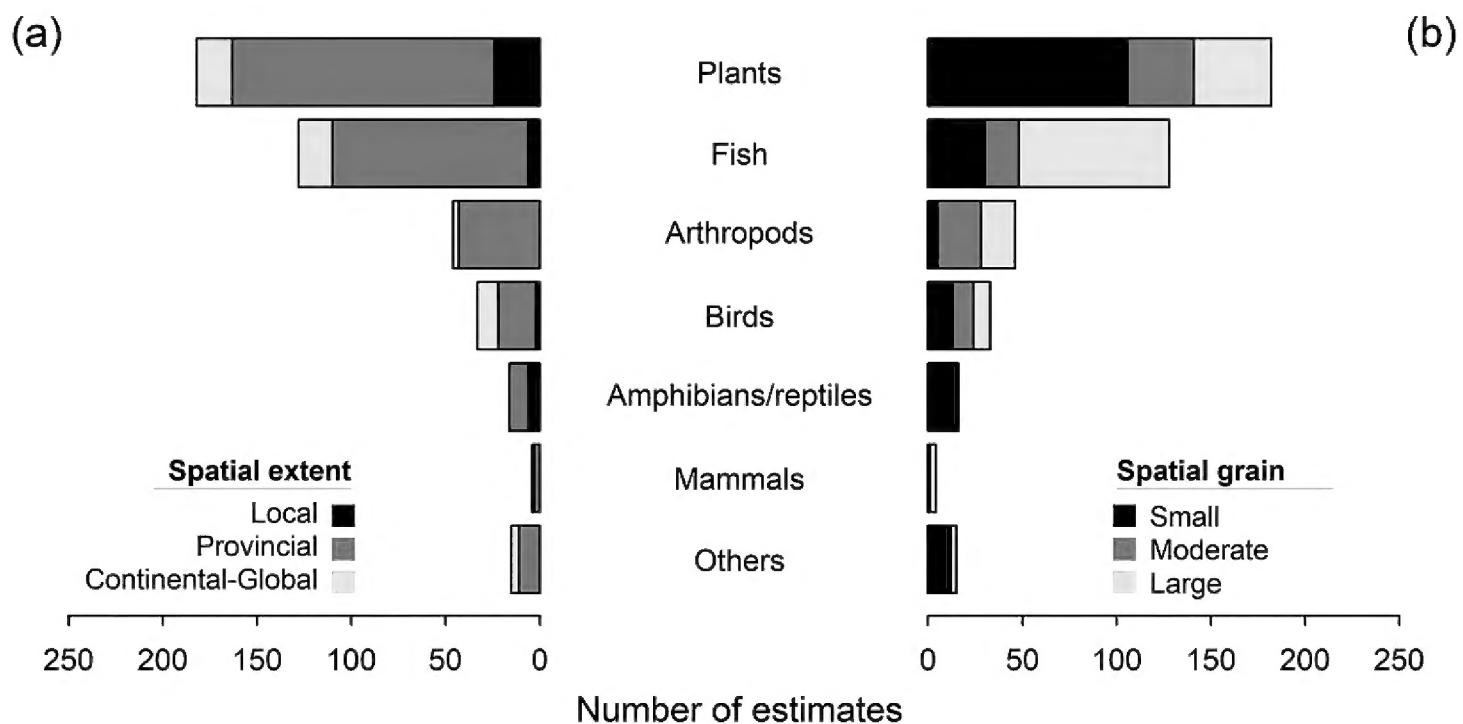


Figure 3. Spatial (a) extent (local < 100 km²; provincial; continental-global) and (b) grain (small < 10 km²; 10 km² ≤ moderate ≤ 1000 km²; large > 1000 km²) of estimates reported in biotic homogenisation articles.

local extents are limited to the study of plants. Moreover, plant studies have largely focused on small spatial grains, whereas fish studies commonly investigate biotic homogenisation at larger grains. Comparative studies have highlighted the scale-dependence of perceived patterns in biotic homogenisation (e.g. Yang et al. 2015). In general, greater levels of homogenisation are expected at coarser spatial grains of investigation because of higher probabilities of recording the same non-native species and lower likelihoods of observing the extirpation of a native species by virtue of a greater total area and diversity of habitats (Olden et al. 2011). Stemming from the fact that the mechanisms responsible for shaping beta-diversity vary from local to regional spatial scales (McGill et al. 2015), a more explicit consideration of spatial scale is called for in future investigations of biotic homogenisation.

Of additional concern is the fact that past investigations of biotic homogenisation have largely focused on reconstructed species pools from published lists of native, extinct and/or non-native species, thus limiting comparisons to be made between some “historical” baseline and the present day (Rosenblad and Sax 2017). This consequently hampers the ability to estimate rates of changes and detect transitory states in both increases (homogenisation) and decreases (differentiation) in similarity. In one interesting example, avian communities of France have become functionally more similar over the past two decades, but they first demonstrated a period of differentiation before exhibiting strong homogenisation in response to range-expanding non-native species (Monnet et al. 2014). A similar pattern was observed for the taxonomic homogenisation of freshwater fish faunas in south-western United States (Pool and Olden 2012). These and other studies, that have quantified changes in similarity over time, point to the importance of understanding lagged species losses (extinction debt) and gains (invasion debts) in response to environmental change. Looking to the future, increasing

availability of “big data” through public repositories and citizen science programmes (Devictor et al. 2010) provides new research opportunities to better understand how patterns in biotic homogenisation manifest across multiple spatial and temporal scales.

Reconcile past and embrace new approaches to quantification

The burgeoning investigation of beta-diversity by ecologists (Anderson et al. 2011) is also reflected in the large variety of approaches used to both describe and quantify biotic homogenisation (Fig. 4). Over 84 % of studies have quantified homogenisation according to species (taxonomic) identity; relatively fewer studies focused on either the functional or phylogenetic facets of this phenomenon. Functional or phylogenetic homogenisation may occur because species invasions and extinction are not random, but are related to intrinsic life-history traits of species that exhibit higher-order phylogenetic affinities (Blackburn and Jeschke 2009). Functional homogenisation reflects a convergence of biotas over time associated with the establishment of species with similar functional ‘roles’ in the ecosystem (e.g. high redundancy of functional forms or traits) and the loss of species possessing a unique combination of traits and/or evolutionary history (Olden et al. 2004). With increasing recognition of the important roles served by some non-native species in contemporary landscapes (Schlaepfer et al. 2011), enhanced focus on understanding the patterns and drivers of functional homogenisation is needed. Studies comparing patterns in taxonomic and functional homogenisation have been particularly intuitive in this regard (e.g. Smart et al. 2006, Pool and Olden 2012, Sonnier et al. 2014, Villéger et al. 2014).

Beta diversity reflects the dual phenomena of spatial turnover driven by species replacement and nestedness resulting from species loss (Baselga 2010). To date, the majority of studies have quantified homogenisation according to broad-sense measures of beta-diversity (e.g. Jaccard, Sorensen indices), making it impossible to disentangle the contributions of spatial turnover and nestedness to observed homogenisation (Fig. 4). Given that changes in community composition may be driven by (Baiser et al. 2012) or occur independently from (Dornelas et al. 2014) changes in species nestedness, the appropriate selection of similarity metrics is paramount (Olden and Rooney 2006). For this reason, it is posited that studies which calculate complementary metrics of beta-diversity are most likely to yield the greatest insights into the process of biotic homogenisation. Until such studies are performed, the ability to broadly understand biotic homogenisation via literature syntheses will only be possible by re-analysing large databases (e.g. Baiser et al. 2012) rather than performing formal meta-analyses of published metric values.

Early studies of biotic homogenisation focused almost exclusively on simple measures of pairwise changes in taxonomic similarity over time, where an increase in similarity provided evidence for homogenisation. However, reported measures were often very modest, with average changes in pairwise similarity commonly hovering around zero and rarely exceeding a couple of percentage values (Olden et al. 2011). For exam-

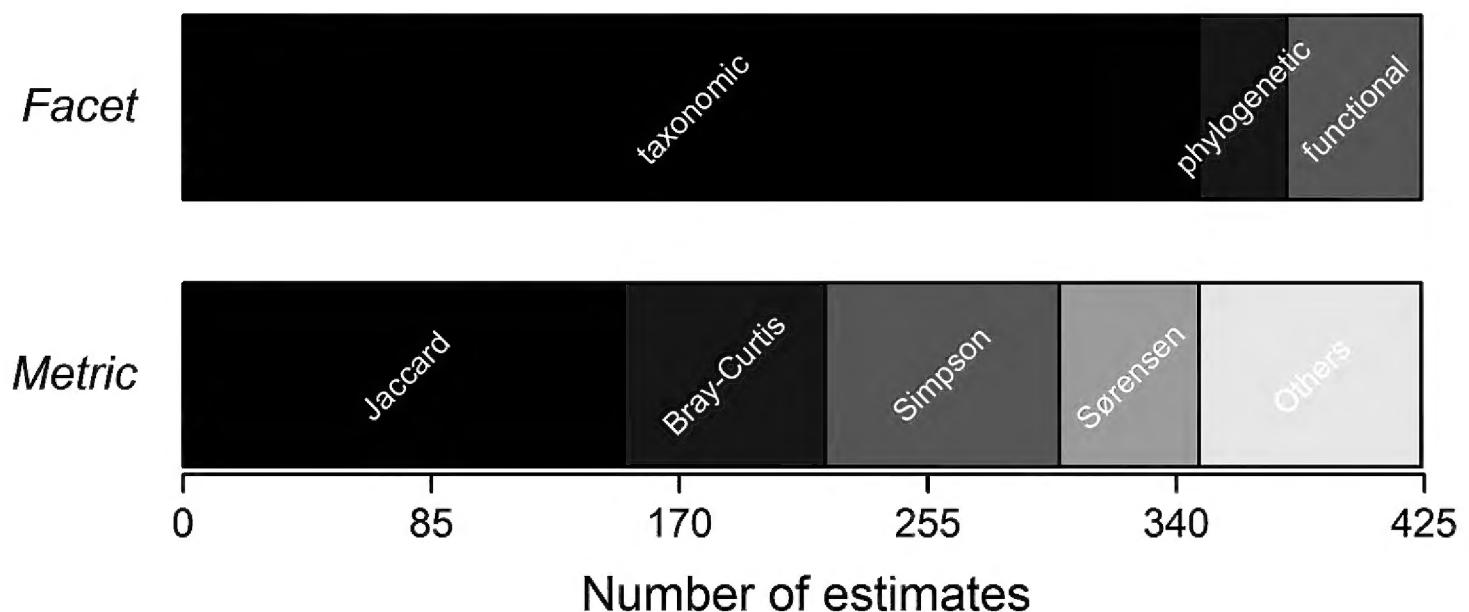


Figure 4. Methodological focus of the biotic homogenisation articles assessed. The facets include *taxonomic* for species-level analyses; *phylogenetic* for phylogenetic diversity metrics according to phylogenetic trees or higher taxonomic ranks; and *functional* according to species-level traits. Biotic homogenisation has been quantified according to presence-absence of species, traits or nodes in the phylogenetic tree (Jaccard, Simpson and Sørensen) or species/trait abundances (Bray-Curtis). Other metrics include the Raup-Crick measure of beta diversity, Morisita-Horn, Euclidean and Gower dissimilarity index and additive and multiplicative definitions of beta-diversity (e.g. β_{Add} , Whittaker's β_W , β_{Shannon}).

ple, studies have reported a 1.3 % increase in fish faunal similarity in Canada (Taylor 2004), a 2.8 % increase in bird community similarity in the Netherlands (Van Turnhout et al. 2007) and a 0.3 % increase in compositional similarity of the continental flora of Chile (Castro and Jaksic 2008). Whether small degrees of homogenisation are greater than expectations based on chance alone remains questionable in many instances. Although the reporting of average similarity change continues today, it is reassuring that both univariate and multivariate tests of significance are increasingly deployed (e.g. Liu et al. 2017, Rosenblad and Sax 2017, Strecker and Brittain 2017) and the use of null models appears to be fruitful despite being under-utilised in the context of homogenisation.

Improve our knowledge of the underlying drivers

Early efforts called for an enhanced process-based understanding of biotic homogenisation (Olden and Poff 2003). Given clear linkages between human activities and species invasions and extinctions, initial attention focused primarily on correlating patterns in homogenisation and urbanisation based on datasets representing heterogeneous environmental settings (i.e. political units or grids) (McKinney 2006). More nuanced investigations quickly followed and yielded divergent results according to the taxa (Kühn and Klotz 2006, Marchetti et al. 2006, Luck and Smallbone 2011), region (La Sorte et al. 2008) and spatial scale addressed (La Sorte et al. 2007, Trentanovi et al. 2013). More recent efforts have considered a broader suite of potential drivers. For example,

logging forest fragmentation was the dominant driver of taxonomic homogenisation in Brazilian Atlantic forests (Lôbo et al. 2011) and phylogenetic homogenisation in Cambodian forests (Toyama et al. 2015), fish faunal homogenisation of Australia was highly concordant with dam infrastructure (Olden et al. 2008) and increasing spring temperatures were associated with bird functional homogenisation in the Czech Republic (Reif et al. 2013). Studies have also demonstrated that natural environmental variability can be an important driver of biotic homogenisation and that changing native species ranges, not the invasion of non-native species, can promote community similarity (e.g. McCune and Vellend 2013, Johnson et al. 2014).

Species assemblages will likely continue to bear the scars of past invasions and extirpations for years to come. However, some positive signs have already emerged. In response to decelerating rates of cropland expansion in large parts of Europe, Carvalheiro et al. (2013) found that species richness loss and biotic homogenisation has slowed and even partially reversed for certain taxa in recent decades. Moving forward, new research that seeks to elucidate temporal change amongst determinants of taxonomic, functional and phylogenetic homogenisation continues to be necessary (e.g. Clavero and García-Berthou 2006, Pool and Olden 2012). Evaluating and comparing drivers of homogenisation across taxa, regions and temporal and spatial scales remains ripe areas for future investigation.

Reveal the conservation implications

Despite the generally acknowledged fact that species diversity loss can result in various ecological, evolutionary and socioeconomic impacts, a robust understanding of the consequences of biotic homogenisation is still conspicuously lacking (Olden et al. 2004). Whereas biodiversity conservation is primarily concerned with maintaining native species diversity at local (alpha-diversity) and/or regional (gamma-diversity) spatial scales, biotic homogenisation describes changes in beta-diversity over time. Maximising beta-diversity is not necessarily desirable for gamma-diversity conservation, because human activities can cause the similarity of local communities to increase, decrease or remain unchanged (Socolar et al. 2016). Therefore, measures of biotic homogenisation in isolation are not sufficient to design or evaluate conservation strategies. However, the homogenisation concept can be applied to monitor temporal changes in the complementarity of conservation reserve networks (Rooney et al. 2007), thus helping achieve efficient conservation solutions by promoting alpha-diversity while simultaneously allowing the representation of gamma-diversity to be maximised (Bush et al. 2016). Taken together, despite the fact that alpha- and gamma-diversity have been the focus of local and regional conservation actions, the adoption of beta-diversity research and, by extension, the study of biotic homogenisation into conservation remains an emerging frontier (Socolar et al. 2016).

The relative dearth of studies quantifying functional and phylogenetic homogenisation (Fig. 4) currently limits the ability to understand how these processes may

compromise community and ecosystem functioning, stability and resistance to environmental change. For example, by both narrowing and synchronising the response diversity of communities, functional homogenisation could compromise the potential for landscape-level buffering of ecosystems to disturbance (Olden et al. 2004). Given continued calls to expand the notion of biodiversity in modern conservation efforts, more dedicated attention to the ecological implications of functional and phylogenetic homogenisation is needed.

Forecast future homogenisation in a rapidly changing world

One of the most pressing challenges is to provide reliable, yet practical, scenarios of future biotic homogenisation. Previous studies have predicted changes in community similarity by assuming that currently unconfirmed non-native and translocated native species would establish self-sustaining populations and native species of conservation concern (i.e. critically endangered, endangered and vulnerable) would be driven to extinction in the future (e.g. Liu et al. 2017). However, spatio-temporal patterns of species extinctions and invasions are likely to change as a result of synergies across multiple human stressors (Urban 2015), thus putting into question these simple extrapolations of community change. In this respect, modelling approaches provide the most flexible way to generate projections of future community changes (D'Amen et al. 2017). Recent methodological developments have increased the potential for including detailed mechanisms (e.g. dispersal, biotic interactions, adaptations) and improving species-specific range projections (Zurell et al. 2016). Community-level models also provide a promising way forward because they facilitate the modelling of all species, including the rare or poorly-sampled ones (Olden 2003), while expanding the possibility to account for the observation process (Iknayan et al. 2014). In the case of incomplete information about species' distributions, trait-based approaches might be the most straightforward solution to provide reliable estimates of future species' extinction risk (Pearson et al. 2014) and spread (Santini et al. 2016) in data-scarce areas. Understanding and projecting real, multi-species community (re)assembly represents a significant challenge, but also a great opportunity to better anticipate future changes in biodiversity.

Conclusion

To many of us, the 'Homogocene' era conjures the prospect of Kunstler's (1993) 'The Geography of Nowhere', where the dissolving of cultural distinction over time threatens the very fabric of society. Indeed, some have likened the process of biotic homogenisation to the now global loss of regional languages, the widespread distribution of fast-food restaurants and the rapid replacement of local businesses by multi-national retailers (Olden et al. 2005). It is now clear that significant effort has been devoted to revealing patterns in biotic homogenisation, but here continued scientific endeavours

are urged for understanding the causes, consequences and conservation implications of this phenomenon. Looking forward, significant progress in the burgeoning study of biotic homogenisation may come from research that tackles the above-articulated propositions by integrating concepts and approaches from ecology, evolutions and conservation across a hierarchy of spatial and temporal scales.

Data accessibility

All datasets are available at: <https://figshare.com/s/68cd3d11f59add7b1b77>.

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